THE GROWTH RINGS IN THE WOOD OF AUSTRALIAN ARAUCARIAN CONIFERS.

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(Plates x-xi.)

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Introduction.

There is a widespread belief that the rings in the wood of Australian trees are not annual. Several circumstances have contributed to this assumption. The continent of Australia has been settled by people from the cool-temperate parts of Europe where many of the trees form fairly definite, yearly rings. In contrast with the cool-temperate parts of Europe and North America, Australia possesses a warmer climate and a more irregular rainfall. As an expression of climatic conditions the rings in the wood of trees grown in the warmer parts of Australia are much more uneven than those in the trees produced in Europe and the Northern United States of America and Canada. It remains for investigation to show to what extent the wood rings of Australian trees are of annual occurrence. This paper is intended as a contribution to the subject, although its scope is not confined to the duration of the rings.

Curiosity as to the age of trees arises from both aesthetic and utilitarian considerations. Admiration of the giants of the forest frequently evokes the question of their age. It is recognized that trees are among the longest-living of all organisms. To the forester, the age of timber-producing trees is an important economic question, as he bases upon it calculations relating to rate of production and cost of timber. In this respect foresters in Australia are at a disadvantage owing to the uncertain age of the constituent trees of the indigenous forests.

In the United States of America a considerable amount of work has been done on the growth rings of trees. In addition to estimating the age of trees, some of the American investigators have employed the growth rings to interpret climatic conditions in the past. The big tree (*Sequoia gigantea*) has been extensively investigated from this point of view and data extending back as far as 1000 B.C. have been compiled from it. While perusing some of the American literature the writer met with observations and conclusions concerning the nature and occurrence of growth rings. As these details are pertinent to the present investigation a very brief summary of them will be given.

A Partial Summary of American Work on Growth Rings.

Ernst Antevs (1925, p. 121) states that it is a well-known fact that young, vigorous trees are relatively far less influenced by external conditions than are old individuals. Rings formed when the trees are very old may for several reasons not be good. Further on (1925, p. 124) he remarks that just as growth rings may be supernumerary, so also may they be less than normal in numbers. One-sided omission of rings in strongly excentric trunks is quite common. The number of elements decreases till the ring wedges out; but growth may also fail in the entire tree. The normal cause of dropped rings is insufficient nourishment.

A. E. Douglass (1919) made tests on trees of yellow pine (*Pinus ponderosa*) at Prescott, Arizona, in order to determine the time of formation of the red or autumn portion of the rings and the causes of the formation of double rings. The curves which he obtained as a result of the work seemed to indicate clearly that the chief cause of doubling is a deficiency of snowfall in the winter months, December to March. Much of the first growth of the trees in the spring must come from the melting of the autumn and winter snows. This appears to mean that if the winter precipitation is sufficient to bridge over the usual spring drought, the growth continues through the season, giving a large single ring which ends only in the usual red growth as the severity of winter comes on. If, however, the preceding winter precipitation has not been entirely adequate, the spring drought taxes the resources of the tree and some red tissue is formed because of deficient absorption in the early summer before the rains begin. When these rains come the tree continues its growth (1919, pp. 17, 18). The normal ring consists of a soft, light-coloured tissue which forms in the spring, merging into a harder, reddish portion which abruptly ends as the tree ceases growth for the year. It is indicated that the red tissue appears as the tree feels lack of sufficient moisture (1919, p. 20).

D. T. MacDougal (1921) investigated the growth of the Monterey pine (*Pinus radiata*) in the grounds of the coastal laboratory at Carmel, California. The seasons in the region are indeterminate as to frost and temperature features, but the rainfall occurs in the winter and growth depends upon the soil supply of water and the rising temperature, with the result that enlargement of the trunks continues until the soil moisture around the absorbing roots is depleted until it forms no more than 6 to 10 per cent. of the total weight (1921, p. 18). MacDougal was able to produce experimentally by irrigation a second layer of wood in a tree in the year 1920. In the early part of the year a layer 5 mm. in thickness was formed. Another layer of equal thickness was added in the later part of the year as a result of irrigation. The irrigation was carried out in July, after the soil moisture content had diminished to 5-7 per cent. Some double rings were observed in the wood of the trees and the investigator assumed that the doubling occurred in a single year, the second layer being caused by autumn rains (1921, pp. 21-3, 25).

Material Used in this Investigation.

Sections from the base of the stems of the following trees were used: a hoop pine (*Araucaria Cunninghamii*) at Crohamhurst; two trees of the same species in the neighbourhood of Gympie; and a bunya pine (*Araucaria Bidwilli*) in the neighbourhood of Gympie. The outer part of a section from the base of a Queensland kauri pine (*Agathis robusta*) at Kin Kin was also utilized.

The section from Crohamhurst was made available through the generosity of Mr. Inigo Jones. The tree was growing in the open. It measured 49 cm. (19·5 in.) in diameter at the base of the stem and attained a height of 22·5 metres (75 feet). The section supplied to the writer was cut at a distance of 45 cm. (18 in.) from the ground. Mr. Inigo Jones states that the area in which the tree grew was swept by a fire in November, 1894, and that the tree was a seedling in 1895. The tree was felled early in June, 1926. It would take at least two years from the time of the fire for the young tree to attain the height of 45 cm., the point at which it was sectioned in 1926. Accordingly the tree could be considered to have existed for a maximum period of 30½ years from the time it reached the point at which it was sectioned until it was felled. The locality is situated about 20 miles from the sea in latitude 27° S. The climate is subtropical in character. According to figures supplied by Mr. Inigo Jones the mean maximum and minimum shade temperatures for the two warmest months of the year, December and January, are about 83° F. and 65° F. respectively. The mean maximum and minimum shade temperatures for the two coolest months, June and July, are about 66° and 45° respectively. The mean annual rainfall is 80 inches.

The material from the neighbourhood of Gympie was obtained through the courtesy of the Provisional Forestry Board of Queensland. It consisted of a section from the base of a hoop pine 53 cm. (21 in.) in stem diameter and 35 m. (117 ft.) in total height, a section from the base of a small hoop pine 7·3 cm. (2·9 in.) in stem diameter and 6 m. (20 ft.) in total height, and a section from the base of a bunya pine 75 cm. (30 in.) in stem diameter and 34 m. (113 ft.) in total height. The sections of the large hoop pine and the bunya pine were from trees of unknown ages. The small section of the hoop pine was taken from a plantation tree 8 years and 5 months old from the time of germination in the seed bed. Gympie is situated about 28 miles from the sea in latitude 26° S. The climate is subtropical in character. The mean maximum and minimum shade temperatures for December and January, as supplied by Mr. G. G. Bond, Divisional Meteorological Officer, are 85° F. and 68° F. respectively; the mean maximum and minimum shade temperatures for June and July are 69° and 42° F. respectively. The mean annual rainfall is 46 inches.

The Kin Kin section is from a Queensland kauri pine 135 cm. (54 in.) in stem diameter and about 36 m. (120 ft.) in total height. The section is from the base of the tree but only represents 27·5 cm. (11 in.) of the radius of the stem from the bark inwards. The locality is situated between Gympie and the sea in latitude 26° S. The climate is similar in a general way to that of Gympie. The mean annual rainfall is 57 inches.

All the localities from which the material was derived are situated in southern Queensland where the three wettest months are January, February and March.

No material of the North Queensland kauri pines (*Agathis Palmerstoni* and *A. microstachya*) was available for investigation.

General Observations upon the Growth Rings of Australian Araucarian Conifers.

The growth rings of the hoop pine, bunya pine and Queensland kauri pine consist of a light-coloured portion, presumably corresponding to the spring and early summer wood, and a darker or brown-coloured portion, presumably corresponding to the late summer or autumn wood. The transition from the light to the dark portion of the rings is generally a gradual one. As there is a marked difference in the temperature of the summer and winter seasons in southern Queensland it is reasonable to assume that the seasonal differences of temperature affect the growth of the wood of the Araucarian conifers under investigation. This consideration leads one to expect that annual rings may be formed by them in some measure at least.

The same degree of distinction and regularity in the growth rings as that characteristic of the wood of European and North American trees such as the English oak (*Quercus pedunculata*), English beech (*Fagus sylvatica*) and Oregon pine (*Pseudotsuga Douglasii*) is not shown by the wood of the subtropical specimens of Australian Araucarian conifers. The wood of the Australian Araucarian conifers contains scattered parts in which closely compressed rings occur and sometimes other scattered parts in which the rings are faint or entirely lacking. Very fine and numerous closely-compressed rings are particularly frequent in the innermost portion of the section of the bunya pine from the neighbourhood of Gympie. On the other hand the outer part of this section and the section of the outer part of the Queensland kauri pine from Kin Kin possess a fairly large number of areas in which the rings are either indistinct or quite lacking. Individual areas of this kind sometimes extend over a radial distance of 1 cm. (0·4 in.).

The fine, numerous and closely compressed rings of the innermost part of the section of bunya pine from the neighbourhood of Gympie may be due to the suppression of the tree in its youth. Suppression is assumed to indicate that the tree was crowded in a rain forest or other dense forest where the sunlight was meagre and growth retarded in consequence. The areas with ill-defined or absent rings in the outer part of the same section and in the section of the outermost part of the Queensland kauri pine from Kin Kin may be the result of successions of mild winters through which growth continued. Very fine rings alternating with broader, more regular ones in the sections of all the trees examined may be due to deficient spring or early summer rains or to the occurrence of warm periods in winter during which growth is reawakened. Deficient spring or early summer rains and comparatively warm periods during the winter months are not rare in southern Queensland. Douglass's work on the yellow pine (*Pinus ponderosa*) in Arizona, where dry springs occur, indicates that insufficient moisture in the early summer causes the formation of a ring in the wood of the trees he studied. In all probability rings are also produced in our conifers by an insufficient moisture supply in very dry springs or very dry early summers.

Of all the sections examined those of the hoop pine (*Araucaria Cunninghamii*) showed the greatest regularity in the occurrence of the rings. Two sections of hoop pine stems are represented by the photograph on Plate x. The ring boundaries are more sharply defined in old and mature trees than in young, fast-growing ones. The most marked uniformity in the breadth of the rings was observed towards the centre of the hoop pine from Crohamhurst and of the large hoop pine from the neighbourhood of Gympie. These sections are shown on Plate x. This circumstance is in accordance with Antevs's statement (1925, p. 121) to the effect that young; vigorous trees are relatively far less influenced by external conditions than are old individuals. The wedging-out or extinction of rings on one side of a tree, which is mentioned by Antevs (1925, p. 124), has been observed by the writer in the section of the bunya pine from the neighbourhood of Gympie. In this case it was associated with the slight excentric development of the stem.

The Occurrence of Annual Rings in Australian Araucarian Conifers.

From the partial summary of American literature given in this paper and from the writer's observations upon the material at his disposal it is concluded that all of the rings appearing in the sections of the Australian Araucarian conifers do not represent the growth of single years. It appears highly probable that two, three or even more rings may be added to the woody cylinder in one year. Instances may also occur in which rings are omitted or are only imperfectly defined. The subtropical climate of the localities in which many of the Australian Araucarian conifers grow and the irregularity of the rainfall at times would appear to induce irregularity in the wood rings. It is to be expected that subtropical representatives of Australian Araucarian conifers would exhibit less uniformity in their wood rings than would coniferous trees in Arizona where there is an annual fall of snow. This yearly occurrence of snow could be anticipated to cause a cessation of growth in winter much more readily than the winter temperatures of subtropical Australia.

On the other hand there is evidence to show that there are rings in varying numbers in the wood of the sections of the hoop pine (*Araucaria Cunninghamii*) each of which was apparently produced in a single year. These rings are assumed to be annual ones. This statement applies only to the sections obtained and prepared for this investigation and more particularly to the section supplied by Mr. Inigo Jones from Crohamhurst. Regular or fairly uniform rings can be traced in about one-half of the Crohamhurst stem. The inner part of the stem shows an unbroken succession of ten fairly regular rings. The remainder of the stem of the same tree shows in places series containing two fairly uniform rings. These series of rings and the ten rings in unbroken succession from the centre of the tree outwards have the appearance of annual rings (see Plate x). As the approximate age of this tree is known, the probability of the fairly regular and serially-connected rings being annual can be tested. For this purpose the radial measurement of the tree was divided by the mean measurement of the width of the rings. If the quotient thus obtained approximates the known age of the tree it provides at least a partial proof that the rings measured are annual ones. By this method 27 was the quotient obtained and, as already stated, the tree had existed for a maximum period of 30½ years from the time it reached the plane in which it was sectioned until it was felled. This result is considered to substantiate, at least partly, the assumption that the fairly uniform rings occurring in succession in several series in the section are of an annual character. The discrepancy between the known age of the tree and its age as calculated by means of the annual rings represents an error of 11·5 per cent.

The same method was applied to the large section of the hoop pine (*Araucaria Cunninghamii*) of unknown age from the neighbourhood of Gympie. This tree measured 53 cm. (21 in.) in stem diameter. The breadth of 35 rings of fairly uniform size and occurring in series was measured. Their mean width was found to be approximately 2 mm. The radius of the stem divided by the mean width of the measured rings resulted in a quotient of 135, which is the estimated age in years of the tree.

This method of estimating the age of coniferous trees in subtropical Australia has its limitations. It can only be applied to examples in which series of fairly regular rings can be observed. Strongly compressed rings cannot be utilized and trees exhibiting excessively irregular rings are unsuitable. It appears probable that the method would minimize the age of a tree. This is deducible from the circumstance that the rings which are used would be those produced in favourable years when growth was continuous from spring to autumn wood.

The section of the bunya pine (*Araucaria Bidwilli*) from the neighbourhood of Gympie is not suitable for estimating the age of the tree from which it was taken. It contains a very large number of closely compressed rings in the inner part and very irregular ones in the outer part.

The part of the section of the base of the stem of the Queensland kauri pine (*Agathis robusta*) from Kin Kin contains a number of fairly regular rings in series. The mean breadth of these rings was found to be 3 mm. It is estimated that this tree produced the outer 27·8 cm. (11 in.) of the radius of its stem in 93 years. If it grew at the same rate during the remaining, earlier part of its life, it is estimated that its total age is 228 years. When felled it was 135 cm. (54 in.) in diameter. Some of the very large trees of the species which once grew at Kin Kin attained a stem diameter of 240 cm. (8 feet). If these trees grew at the same rate as the one from which the section under investigation was taken, their age could be estimated at about 400 years. It is obvious that these estimates require more material for their confirmation or otherwise, as they are based on very meagre evidence.

In concluding this section of the paper it should be remarked that the subject of the occurrence of annual rings in Australian trees is worthy of further investigation. Although the study of wood rings in subtropical trees is of considerable interest both from the scientific and economic aspects, it might be anticipated that more definite conclusions could be formulated from an investigation of the rings in the wood of trees grown in the cooler parts of the continent.

Microscopic Features of the Growth Rings.

The rings in the wood of young, fast-growing trees are frequently more readily discernible to the unaided eye than by microscopic examination of thin, transparent sections. This conclusion was arrived at after studying the rings of the young hoop pine (*Araucaria Cunninghamii*) from the Forestry plantation in the neighbourhood of Gympie. Some difficulty was experienced in tracing in stained microtome sections rings which were visible to the unaided eye in smoothed sections of the stem of the tree. It is therefore evident that some of the rings in examples of this kind are not sharply defined in a microscopic sense. The growth rings in the wood of mature trees of hoop pine (*Araucaria Cunninghamii*) and bunya pine (*A. Bidwilli*) from Gympie and in the wood of the Queensland kauri pine (*Agathis robusta*) from Kin Kin are traceable in microtome sections. The photomicrographs reproduced on Plate xi show the minute structure of the rings. The most obvious microscopic feature consists of the reduction of the transverse measurement of the tracheids of the outer or brown portion of the rings corresponding in appearance to autumn or late summer wood. These tracheids are also characterized by their thicker walls. This thickening consists of an extension of the secondary cell wall or that part of the wall in which the greater amount of lignification, or transformation into wood, takes place.

Another feature of the outer or brown portion of the rings is the presence of bordered pits in the tangential walls of the tracheids. By far the greater number of bordered pits is situated in the radial walls. E. C. Jeffrey (1917) states that the tangential pits are characteristic of the end of the annual rings in conifers and that this condition is notable for example in tropical or subtropical species of the genus *Araucaria*. Tangential pitting has been observed by the writer in the outer or brown portion of the rings in the wood of the hoop pine, bunya pine and Queensland kauri pine. They are much more frequent in the Queensland kauri pine than in the two species of *Araucaria*. They are much smaller and much less prominent than the numerous bordered pits in the radial walls of the tracheids.

This observation applies to the hoop pine, bunya pine and Queensland kauri pine. The pits of the tangential walls of the tracheids are bordered ones. In the bordered pits in the tangential walls of the outer portion of the rings of the Queensland kauri pine, the middle lamella between the opposite apertures is considerably thickened and has the appearance of an extended torus. The thickened portion of the middle lamella stains intensely with iron-haematoxylon and is responsible for much of the darkened appearance of the tangential bordered pits shown in Fig. 3, Plate xi.

It has not been possible for the writer to show that the rings in which the tangential pitting is seen are of an annual character. This kind of pitting was observed chiefly in mature trees of unknown age. Some of the rings in which it was seen were very narrow ones and might have been formed as the result of lack of moisture in November or December. A ring of this kind is shown in Fig. 1 of Plate xi. It is situated towards the middle of the picture between two larger rings and its outer or brown portion consists of only one or two rows of tracheids with thickened walls. Examination of microtome sections of the small plantation tree of known age from the neighbourhood of Gympie shows that the tangential pitting is exceedingly rare in this specimen. This kind of pitting could not be traced in transverse sections in this instance, although similar sections from mature trees showed it. Only in one or two rings of the small plantation tree could the tangential pitting be traced in radial sections. It would therefore appear that young fast-growing trees of the hoop pine do not develop tangential pitting in the walls of the tracheids of their wood to the same extent as mature trees do.

Summary.

Sections of stems of the hoop pine (*Araucaria Cunninghamii*), bunya pine (*Araucaria Bidwilli*) and Queensland kauri pine (*Agathis robusta*) were examined. All of the sections were obtained from trees growing in localities in which the climate is of a subtropical character. The same degree of distinction and regularity in the growth rings as that which characterizes the wood of many European and North American trees is not shown by the wood of the subtropical specimens of Australian Araucarian conifers.

Of all the sections examined those of the hoop pine showed the greatest regularity in the occurrence of the rings. The boundaries of the growth rings are more sharply defined in old, mature trees than in young, fast-growing ones. The most marked uniformity in the breadth of the rings was observed towards the centre of the sections of the hoop pine from Gympie and Crohamhurst. This circumstance is in accordance with the statement by Antevs to the effect that young, vigorous trees are relatively far less influenced by external conditions than are old individuals.

It appears highly probable that two, three or even more rings may be added to the woody cylinder in one year. Instances may also occur in which rings are omitted or are only imperfectly defined. On the other hand there is evidence to show that in the sections of the hoop pine there are rings in varying numbers, each of which was apparently produced in a single year. Rings of fairly uniform size arranged in connected series in a section of a hoop pine tree from Crohamhurst are assumed to be annual ones. Partial proof of this assumption is given. The radial measurement of the stem of the tree when divided by the mean measurement of the breadth of the assumed annual rings gave a quotient approximating

the known age of the tree. It is suggested that this method could be applied in estimating the age of trees in which a number of fairly uniform rings arranged in series occurs. The method is applied to a section of a hoop pine tree from the neighbourhood of Gympie and part of a section of a Queensland kauri pine tree from Kin Kin and an estimated age for the trees obtained.

The rings in young, fast-growing trees are frequently more readily discernible by the unaided eye in smooth, opaque sections than by microscopic examination of thin, transparent sections. The microscopic features of the growth rings are outlined and illustrated. Bordered pits in the tangential walls of the tracheids are confined to the outer or brown portion of the rings in the hoop pine, bunya pine and Queensland kauri pine. The bordered pits in the tangential walls of the tracheids are much more frequent in the Queensland kauri pine than in the hoop and bunya pines.

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EXPLANATION OF PLATES X-XI.

Plate x illustrates the smoothed parts of sections of the mature hoop pine (*Araucaria Cunninghamii*) from the neighbourhood of Gympie (on left) and of the tree of the same species from Crohamhurst (on right). The entire radius of the stems is shown in each case. The centimetre scale on the right lower side shows the extent of reduction of the illustrations in both cases. The lines drawn into the section on the right indicate roughly the limits of the rings assumed to be annual ones. The section on the right is from a tree 30½ years old. Using the assumed annual rings as a basis of calculation the age of this tree is estimated at 27 years. The actual age of the tree represented on the left is not known, but, using assumed annual rings as a basis, its age is estimated at 135 years.

Plate xi.—In all of the figures the honeycomb-like pattern represents the tracheids in cross section. The dark, narrow, double lines passing from top to bottom of the pictures represent the wood rays. These two tissue elements, tracheids and rays, are the sole constituents of the normal wood of the species of *Araucaria* and *Agathis* which are dealt with.

Figs. 1 and 2 were photographed with a 16 mm. apochromatic objective (N.A., 0·3) and compensating eyepiece 4. Fig. 3 was photographed with a 4 mm. apochromatic objective (N.A., 0·95) and compensating eyepiece 4. The sections were stained with Heidenhain's iron haematoxylon and safranin.

Fig. 1.—Photomicrograph of transverse section of wood of hoop pine (*Araucaria Cunninghamii*). The figure illustrates the three outermost growth rings of the specimen shown on the left of Plate x. The uppermost portion of the figure is turned towards the bark. Three growth rings are shown. The very narrow one towards the middle of the figure might have resulted from a dry early summer, but no proof of this assumption can be given. × 40.

Fig. 2.—Photomicrograph of transverse section of portion of wood of bunya pine (*Araucaria Bidwilli*) from neighbourhood of Gympie. A growth ring is seen towards the middle of the figure. × 40.

Fig. 3.—Photomicrograph of transverse section of portion of wood of Queensland kauri pine (*Agathis robusta*) from Kin Kin. A growth ring is shown obliquely traversing the middle of the figure. The small dark spots on the tangential walls of the thickened tracheids indicate the positions of tangential bordered pits. The two loop-like structures in the radial wall of a tracheid in the upper left side of the figure indicate the positions of two radial bordered pits. The dark band on the left represents a wood ray. × 170.

APPENDIX: *Growth Rings in an Australian Fossil Coniferous Wood.*

Through the courtesy of Mr. H. A. Longman, the writer was able to examine a specimen of a fossil, apparently coniferous wood collected in a cutting in Ann Street, Brisbane. Professor Richards determined the beds, in which the fossil was found, as situated at the base of the Ipswich Coal Measures (Triassic). A hand-specimen of the fossil wood was ground down to a smooth surface on a transverse plane. Examination with a lens showed well-defined tracheids in cross section and rays in longitudinal section. Wood rings are very well marked in the specimen. They vary in width from 1 to 2 mm. and are more regular than the rings in the wood of the present-day Queensland conifers which were examined during the investigation outlined above. The growth rings in the fossil wood in regularity approach those in the wood of many European and North American trees which are contrasted in this particular with the subtropical Australian Araucarian conifers. A small piece of the fossil wood was placed on the stage of a microscope and a connected series of four rings measured with an ocular micrometer. The measurements of the width of the rings obtained in this way were: 1·52, 1·36, 1·6 and 1·6 mm. Viewed from the standpoint of living trees the rings in the fossil wood have the appearance of being annual in character. The regularity of the rings suggests that the climate in Triassic times might have been much more regular in the incidence of seasonal factors, such as rainfall, than the climate of Brisbane at present. If the rings were annual in occurrence it is also indicated that the tree which became fossilized grew at a slower rate than the Araucarian conifers dealt with in the paper above (see section on the occurrence of annual rings in the wood of Australian Araucarian conifers).

In Bulletin No. 7 of the Geological Survey, Department of Mines, Queensland, p. 15, 1898, John Shirley has described a fossil wood under the name of *Araucarioxylon Brisbanense* from the locality "Ann Street, North Brisbane, in street cutting; Gympie Formation, Permo-Carboniferous System". The specimen described by Shirley is evidently from the same beds as the specimen examined by the writer. Shirley's specimen may be from the same species and possibly from the same tree. Our knowledge of the stratigraphy of this locality is now such that we are reasonably certain that the fossil-wood-bearing beds in Ann Street are at the base of the Ipswich Coal Measures (Triassic), and do not belong to the Permo-Carboniferous System.